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The Description of Euceroptrinae, a New Subfamily of Figitidae (Hymenoptera), including a Revision of *Euceroptres* Ashmead, 1896 and the Description of a New Species

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Abstract.—The figitid genus *Euceroptres* Ashmead has recently been determined to render the Thrasorinae, a subfamily where the genus is currently classified, paraphyletic. To maintain the monophyly of Thrasorinae, *Euceroptres* is here redescribed and placed in its own subfamily, Euceroptrinae. All known species are redescribed and a new species is described; a lectotype is designated for *E. primus* Ashmead, 1896. The phylogenetics of Euceroptrinae, Parnipinae, Plectocynipinae and Thrasorinae are discussed, and the hypothesis that ancestral lineages of figitids attacked gall-inducing Hymenoptera is supported. Agastoparasitism among these lineages appears to be plesiomorphic. Though branch support is relatively low for inferring the precise branching order of the gall-inducer parasite lineages, the classification of problematic species is much improved.

Resolving the early branching events separating the phytophagous Cynipidae from the entomophagous Figitidae (Hymenoptera: Cynipoidea) continues to challenge hymenopterists. Although cynipoids resolve phylogenetically within the entomophagous parasitoid Hymenoptera (Ronquist et al. 1999, Dowton and Austin 2001), the majority of Cynipidae are obligate phytophages, inducing spectacular galls on host plants in 17 families of angiosperms (Weld 1952, Liljeblad and Ronquist 1998, Ronquist 1999). Figitids associated with the gall community are important for understanding the early evolution of these lineages; Ronquist (1995a, 1999) and Buffington et al. (2007) discussed two ancestral groups of cynipoids, i.e., Parnipinae and Thrasorinae, that represent lineages whose biology lie somewhere between entomophagy and phytophagy. Further, these lineages also represent figitid agasotoparasites (parasitoids whose primary hosts are themselves close relatives (Ronquist 1994)), a life-history strategy rare among Figitidae. Hence, understanding the taxonomy, biology, and phylogenetics of these groups will elucidate the evolutionary origins of the phytophagous cynipid lineage.

The Thrasorinae have been the subject of a few recent studies attempting to clarify our accumulated knowledge on this group. Ronquist (1994) grouped several cynipoid genera together in what he called the 'figitoid inquilines'; later, in Ronquist (1999), these genera (*Euceroptres* Ashmead, *Thrasorus* Weld, *Myrtopsen* Dettmer, *Pegacynips* Brèthes and *Plectocynips* Diaz) were placed within Thrasorinae, a group that previously only contained *Thrasorus* (Kovalev 1994). Ros-Farré and Pujade-Villar (2007) removed *Pegacynips* and *Plectocynips* from Thrasorinae and placed them into the newly described Plectocynipinae, and de-

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scribed a new thrasorine genus, *Scutimica* Ros-Farré. 'Buffington (submitted) revises the Australian Thrasorinae and describes a new genus of thrasorines associated with galls on *Eucalyptus* spp.'

Ronquist (1999) suggested the placement of *Euceroptres* within Thrasorinae as tentative at best, given that the taxon lacks a number of synapomorphies the remaining taxa possess. In both Ros-Farré & Pujade-Villar (2007) and Buffington (submitted), *Euceroptres* Ashmead was determined not to be a thrasorine, leading Buffington (submitted) to render the taxon *incertae sedis*. Buffington et al. (2007) found weak support for *Euceroptres* to be included within Thrasorinae. Further, *Euceroptres* rendered Thrasorinae paraphyletic if morphological data were excluded. Based on the total evidence phylogeny of Buffington et al. (2007), if Plectocynipinae is recognized, Thrasorinae is rendered paraphyletic unless *Euceroptres* is excluded.

MATERIALS AND METHODS

Rearing methods.—Fully developed galls were collected by us from *Quercus agrifolia* NŽe (Fagaceae) in Eaton Canyon State Park, Pasadena, CA. All leaves were removed and bare galls were placed together with tissue paper in plastic zipper bags to collect emerging wasps. Non-reared material for examination was borrowed from institutions listed below.

Descriptions.—Morphological terminology follows that of Ronquist and Nordlander (1989), Fontal-Cazalla et al. (2002) and Buffington et al. (2007); cuticular surface terminology follows that of Harris (1979). Specimens were examined using a Leica Wild M10 with fluorescent lighting. Images for figures were obtained using an EntoVision Imaging Suite, which included a firewire JVC KY-75 3CCD digital camera mounted to a Leica M16 zoom lens via a Leica z-step microscope stand. This system fed image data to a desktop computer where Cartograph 5.6.0 (Microvision Instruments, France) was used to capture a fixed number of focal planes (based on magnification); the resulting focal planes were merged into a single, in-focus composite image. Lighting was achieved using an LED illumination dome with all four quadrants set to 99.6% intensity. Scanning electron micrographs of *Euceroptres montanus* Weld were made by the second author and were downloaded for this study from Morphbank (http://morphbank.net). All images generated during this study are available under the Morphbank ID 195606.

Phylogenetic analysis – matrix.—The matrix used in Buffington et al. (2007) was complemented with the addition of *Ibalia anceps* Say (Ibaliidae). This taxon was included to serve as an additional outgroup to the liopterids (see Ronquist 1999). Sequence data for the ibaliid was downloaded from GenBank (DQ012642, DQ012641, DQ012599, AY621150, EF032242, EF032274). Precisely the same gene regions were used as they were in Buffington et al. (2007); alignments used herein were based entirely on the structural model (Gillespie 2004, Gillespie et al. 2005) proposed for Cynipoidea (Buffington et al. 2007) and included all genetic data; regions of ambiguous alignment were aligned by eye. The model as proposed in Buffington et al. (2007) was not altered by the inclusion of the ibaliid. Morphological and biological characters described in Buffington et al. (2007) were included and used to code *Ibalia anceps*. The final molecular and morphological matrix is available from Treebase (ID SN3726). It should also be noted that Buffington et al. (2007) included a taxon identified as '*Myrtopsen* sp.' from Colombia; this taxon is, in fact, *Scutimica flava* Ros-Farré & Pujade-Villar.

Phylogenetic analysis – parsimony and Bayesian inference.—The structurally aligned total evidence matrix was analyzed based on Buffington et al. (2007); the differences are the addition of *Ibalia anceps* in all analyses, and the Bayesian analyses were run for 5 million generations, sampling every 100 generations and burn-in set to 350 (2.5 million generations and burn-in

set to 250 generations in Buffington et al. (2007)).

List of Depositories.—

AMNH American Museum of Natural History, New York, NY, USA.
USNM National Museum of Natural History, Washington DC, USA.
UCRM Entomology Research Museum, UC Riverside, Riverside, CA, USA.

DESCRIPTIONS

Euceroptrinae Buffington and Liljeblad, new subfamily

Type genus: *Euceroptres* Ashmead, 1896

Diagnosis.—The areolet in the fore wing (ARE, Fig. 1D), lack of a hairy ring at the base of the metasoma, lack of a circumtorular impression and well-developed lateral pronotal carina (LPC, Fig. 1A) differentiate this group from Thrasorinae and Plectocynipinae. Nearly all other species of Figitidae have a smooth mesoscutum (save for notauli) whereas the mesoscutum in Euceroptrinae is transversly carinate to rugulose; the only other figitid groups with a transversly carinate mesoscutum are some Aspicerinae (e.g. *Anacharoides* Cameron, *Callaspidia* Dalhbom, *Omalaspis* Giraud and *Pujadella* Ros-Farré) but these species have a sinuate posterior margin of tergum 2 of the metasoma, and are parasites of Syrphidae (Diptera). Parnipinae bears the closest resemblance to Euceroptrinae, but there are several key differences, including the lack of a mesopleural furrow in Parnipinae (complete in Euceroptrinae (F, Fig. 1B)). Parnipinae are Palearctic parasitoids of *Barbotinia* (Cynipidae: Aylacini) on *Papaver* (Papaveraceae) and Euceroptrinae are Nearctic parasitoids of Cynipini (*Andricus* gall inducers) on *Quercus* spp. (Fagaceae) (summarized in Table 1).

Description.—Body color black to pale orange; legs orange proximally, darker distally. Female with 12–14 antennal segments; male with 15 segments, first flagellomere laterally excavated. Lateral pronotal carina (LPC, Fig. 1A) well developed. Mesoscutum ranging from transversly carinate to rugulose; notauli present, well developed; median mesoscutal impression (MMI, Fig. 1C) present, extending up to ¼ length of mesoscutum; scutellum rugulose, posteriorly rounded (Figs 2A–C). Fore wings hyaline, areolet present (ARE, Fig. 1D). Anterior margin of tergum 3 (T3) of metasoma glabrous; T4–T7 with micropores (MP, Fig. 1F) (reduced in some species).

Euceroptres Ashmead, 1896: Trans. Am. Entomol. Soc., v. 23, p. 187.

Type species: *Euceroptres primus* Ashmead, 1896 (by monotypy).

Included species: *Euceroptres primus* Ashmead.
Euceroptres maritimus Weld, 1926.
Euceroptres montanus Weld, 1926.
Euceroptres whartoni Buffington & Liljeblad, new species.

Diagnosis.—Differs from nearly all other Figitidae by the presence of the areolet in the fore wing (Fig. 1D); the only other group of Figitidae with an areolet is *Parnips* (Parnipinae), but this group lacks a mesopleural furrow. The presence of a well-developed lateral pronotal carina is a plesiomorphic trait within Cynipoidea (Ronquist 1995b, 1999 Ronquist and Nieves-Aldrey 2001, Fontal-Cazalla et al. 2002, Buffington et al. 2007, Liu et al. 2007), and this trait is useful for separating *Euceroptres* from other figitids; among the figitids with this character is *Parnips* (Ronquist and Nieves-Aldrey 2001), all Aspicerinae except *Melanips* (Buffington et al. 2007) and some members of the *Gronotoma* group of Eucoilinae (Fontal-Cazalla et al. 2002, Buffington et al. 2007). Aside from *Parnips*, none of these aforementioned taxa are reared from cynipid galls but are instead reared from cyclorrhaphous Diptera (Ronquist 1999, Buffington et al. 2007). Further, Eucoilinae all possess a scutellar plate with a glandular release pit and nearly all Aspicerinae (except *Melanips*) have a sinuate posterior margin of T-3 of the metasoma (Ronquist 1999, Buffington et al. 2007).

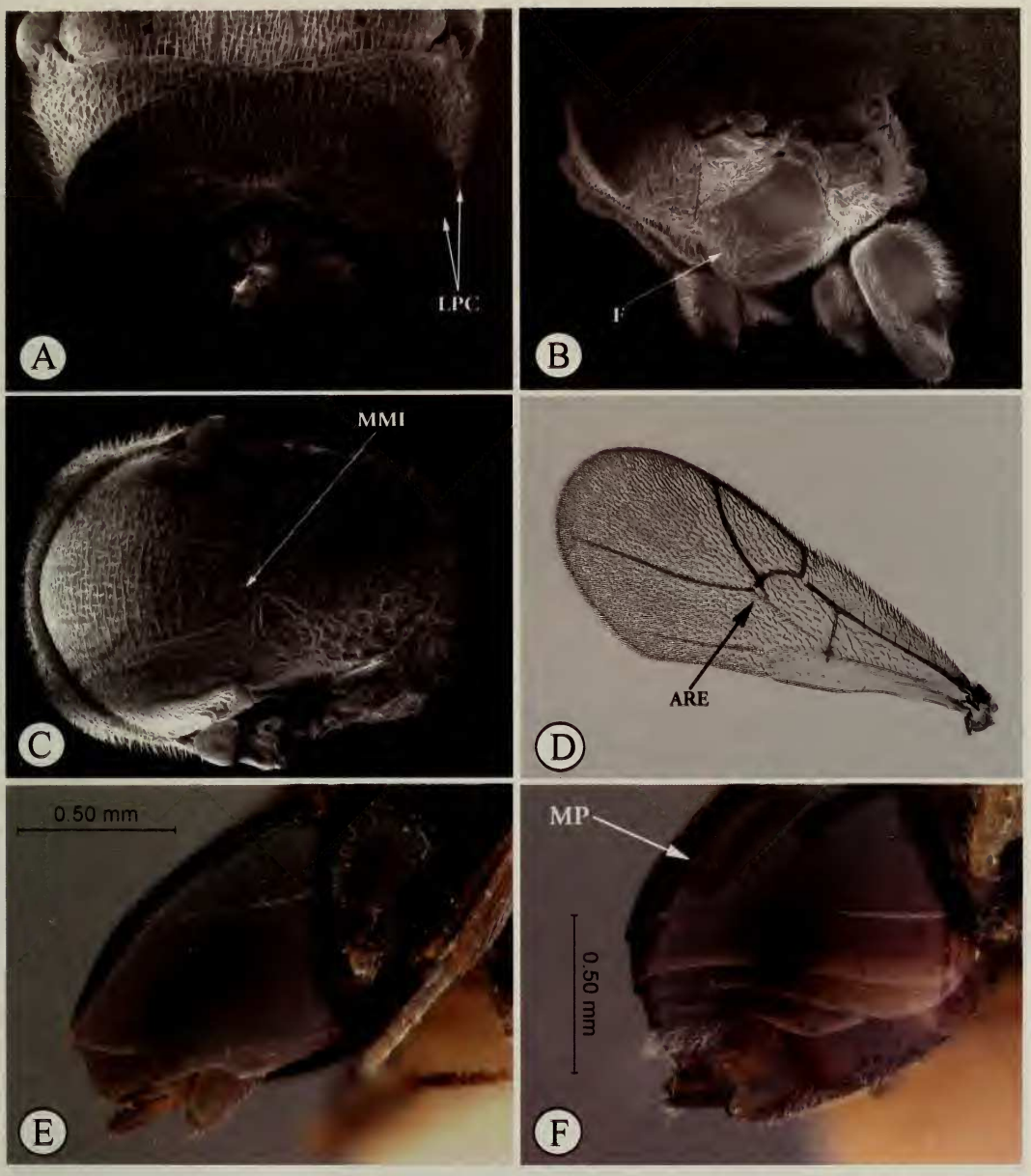

Fig. 1. A–C, F: *Euceroptres montanus* Weld; D: *E. maritimus* Weld; E: *E. whartoni* n. sp. A, mesosoma, anterodorsal view; B, mesosoma, lateral view; C, mesosoma, dorsal view; D, forewing, dorsal view; E–M, female metasoma, posterolateral view. Abbreviations: LPC, lateral pronotal carina; F, mesopleural furrow; MMI, median mesoscutal impression; ARE, areolet; MP, micropore.

Redescription.—**Female. Head.** Black to rusty orange; frons rugulose, densely setose; malar space costulate ventral of eye, rugulose approaching mandibular base; gena and vertex costulate, covered in short appressed setae (Fig. 2A–D); gena broadly rounded (Fig. 2A–C). Antenna basally orange, distally ranging from orange to dark brown, non-clavate; scape 2.25-3× length of radicle, short appressed setae on all flagellomeres, 10–12 flagellomeres present, moniliform (Fig. 2E–F);

Table 1. Species of *Euceroptres*, their gall wasp hosts and oak hosts.

Euceroptres	*Andricus* gall wasp host	Oak host species and section
E. maritimus	*A. quercussuttoni*	*Q. agrifolia*, Erythrobalanus
E. montanus	*A. truckeensis*	*Q. chrysolepis*, Protobalanus
E. primus	*A. quercusflocci*, *A. quercusfutilis*	*Q. alba* (*Q. stellata*), Quercus
E. whartoni	*A. quercusoperator*	*Q. nigra*, Erythrobalanus
	(*A. quercuspetiolicola*)[1]	(*Q. alba*, Quercus)[1]

1. Dubious host record

Fig. [illegible] A and E: *Euceroptres primus* Ashmead; B and F: *E. maritimus* Weld; C and D: *Euceroptres whartoni* n. sp. A–C, [illegible]soma, dorsal view; D, mesosoma, lateral view; E–F, habitus, female.

apical segment 2× length of subapical segment.

Mesosoma. Lateral surface of pronotum deeply rugulose, densely covered in stiff, moderately long setae (Fig. 1A–B); lateral pronotal carina (LPC, Fig. 1A) well developed, extending from lateral margin of pronotal plate to ventral margin of anteroventral inflection of pronotum (Fig. 1A); lateral margins of pronotal plate indistinct; submedial pronotal depressions deep, open laterally (Fig. 1A). Mesopleuron costulate to rugulose anteriorly, setose; mesopleural furrow composed of rugae (F, Fig. 1B); mesopleural triangle deeply impressed, setose, clearly defined along all edges (Figs 1B & 2D); area posterior of mesopleural triangle and dorsal of mesopleural furrow highly polished, glabrous (Figs 1B & 2D). Mesoscutum transversely carinate to rugulose, moderate to densely setose; anteroadmedian signum present; median mesoscutal impression present, ranging from short, notch-like to ¼ length of mesocutum; notauli complete, originating at anterior end of parascutal impression, gradually becoming wider posteriorly (Figs 1C & 2 A–C). Disk of scutellum heavily rugulose, evenly setose (Fig. 2 A–F); scutellar ridge separating scutellar fovea narrow, short; scutellar fovea oval, obliquely angled relative to midline, posterior rim present, center gently rugulose, sparsely setose (Figs 1C & 2A–C).

Metapleural-propodeal complex. Metapleuron and propodeum ranging from glabrous to completely covered in long setae; anterior margin of upper metapleural area jutting-out laterally, glabrous (Fig. 1B); setal pit at ventral margin of metapleuron present; posterior aspects of propodeum smooth to gently rugulose, flat; propodeal carinae thin, complete, parallel; area between propodeal carinae glabrous to setose, with dense, felt-like setae under long, thin setae. Nucha short, glabrous, deeply striate.

Fore wing. Marginal cell closed along anterior margin (Fig. 1D); distinct break present in vein proximal to marginal cell (Fig. 1D); areolet present (ARE, Fig. 1D); marginal and cubital veins represented by trace veins; short setae present on wing surface and along margins.

Legs. Femora orange, tibiae orange to dark brown; sparse, appressed setae present on all femorae and tibiae. Tarsomeres orange-yellow to brown, covered in short, appressed setae (Fig. 2E–F).

Metasoma. Ranging from black or brown to orange; petiole frequently obscured by anterior margin of T3. Posterior margins of T3 and T4 parallel, angled obliquely at 45 degrees relative to horizontal, subequal in length; remaining terga short, telescoped within T4; T4–T9 with micropores (MP, Fig. 1F) though significantly reduced to absent in some species; setae frequently present on T8.

Male. As in female but with 13 flagellomeres; flagellomere 1 as long as fourth antennal segment, laterally excavated, expanded slightly on distal end.

Distribution. Nearctic Region: United States of America: AZ, CA, DC, FL, MA, MD, OR, TX, VA.

Biology. Parasitoids of species of *Andricus* (Cynipidae: Cynipini), which are gall inducers on various species of oak (*Quercus* spp.).

KEY TO SPECIES OF *EUCEROPTRES* (FEMALES AND MALES UNLESS OTHERWISE NOTED)

1. Females with 11 flagellomeres. Metasomal terga 3 – 8 with significantly reduced to absent micropores (Fig. 1) (collected East of the Rocky Mountains) 2
- Females 10 or 12 flagellomeres. Metasomal terga 3 – 8 with well developed micropores (MP, Fig. 1F) (collected West of the Rocky Mountains) 3
2. Median mesoscutal impression short, notch-like . . . . . *Euceroptres primus* Ashmead

- Median mesoscutal impression elongate, often 1/4 to 1/3 length of mesoscutum . . . . . *Euceroptres whartoni*, new species

3. Females with 10 flagellomeres. Dense, felt-like setae present in mesopleural triangle and setal pits between propodeal carinae (Fig. 1B). Area of episternum posterior to anterodorsal margin of metepisternum gently crenulated . . *Euceroptres maritimus* Weld

- Females with 12 flagellomeres. No felt-like setae present. Area of episternum posterior to anterodorsal margin of metepisternum smooth and glabrous . . . . . *Euceroptres montanus* Weld

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Euceroptres maritimus Weld, 1926
Figs 1D & 2B, F

Diagnosis.—Females readily distinguished by having 10 flagellomeres (all other species with either 11 or 12). Separated from *E. primus* and *E. whartoni* by the presence of well-developed micropores on the metasoma (cf. MP, Fig. 1F); this trait is also shared with *E. montanus*. Males and females have dense felt-like setae present in the mesopleural triangle, the setal pits of the metapleuron and between the propodeal carinae; all other species have setae in these areas, but they are not dense and felt-like.

Redescription.—**Female**. As in description of genus, with antennae of female 12 segmented (10 flagellomeres); median mesoscutal impression deep, short, notch-like (Fig. 2B); mesoscutum distinctly transversely rugulose across entire surface; dorsal-anterior margin of mesoplueron umbilicate-rugulose, transitioning to rugulose ventrally; mesopleural triangle with dense, felt-like setae; metapleuron evenly covered with long setae except episternal area posterior to anterior impression of metepisternum, smooth, glabrous; felt-like setae in ventral setal pit; metasomal T4–T9 with distinctly visible micropores (cf. Fig. 1F), dense setal band present along posterior margin of T8; metafemora orange; metatibia medially orange, laterally dark brown; pro- and mesotarsomeres dark orange to brown; metatarsomeres dark brown or black.

Male. As in female but with 13 flagellomeres; flagellomere 1 as long as fourth antennal segment, laterally excavated, expanded slightly on distal end.

Material examined.—Holotype. [first label] "Berkeley, Calif 4/20/12" [20 April 1912], [second label] "Mrs. G.D. Louderbeck", [third label] "1601", [fourth label] "*Quercus agrifolia*", [fifth label] "Type 27299, U.S.N.M.", [sixth label] "*Euceroptres maritimus* Weld". The holotype is a female in good condition, deposited in the USNM. *Additional material.* Allotype. Same data as holotype, 1 male (USNM). Paratypes. USA: *CALIFORNIA*. **Alameda Co.** Same data as holotype, 1 female; Oakland. Bred by Bassett from galls collected by W.M. Beutenmueller, Beutenmueller Coll., received 1935 [no other data available], 1 male (USNM). **Los Angeles Co.**, Santa Anita, Hopkins File number 15605^{s}, June 17–18 1918, reared from *Quercus agrifolia*, collected and bred by L. Weld, 1 female (USNM). **Alameda Co.**, 'through C.V. Riley', [no other data available], 4 males, 3 females (USNM). Non-types. USA: *CALIFORNIA*. **Alameda Co.**, Berkeley, gall collected 10 Mar 1928 from *Quercus agrifolia*, emerged 15 May 1928, W. Ebeling, coll., 3 males, 3 females (AMNH). **Los Angeles Co**. Pasadena, gall collected 22 Feb 1920 from *Quercus agrifolia*, Kinsey Coll., ex gall of *Callirhytis polythyra* Bassett, 23 males, 46 females (AMNH); Claremont, Metz Coll., acc 5635 [no other data available], 1 male (AMNH); Eaton Canyon State Park.,19.IV.2004, ex gall on *Quercus agrifolia*, M. Buffington & J. Liljeblad, 12 males and 15 females (1 male, 1 female under voucher 56737, UCRM; remaining specimens in USNM). *OREGON*. **Josephine Co.**, Grants Pass, coll #8536, taken from *Quercus* spp., [no other data available], 5 males, 13 females (AMNH).

Note: Weld (1926) recorded that part of the paratype series was sent to the USNM under the Hopkin's number 15605^{s}, which was supposedly collected in Montecito, CA

(near Santa Barbara); the specimen in USNM bearing this Hopkin's number is labeled as being collected in Santa Anita, CA (near Pasadena), not Montecito.

Distribution.—Western United States, from southern Oregon in the north to southern California in the south.

Biology.—Reared from the cynipid *Andricus quercussuttoni* (Bassett) on *Quercus agrifolia* Née.

Euceroptres montanus Weld, 1926
Fig. 1A–C, F

Diagnosis.—Females readily distinguished from other *Euceroptres* species by the possession of 12 flagellomeres. Males can be distinguished from *E. maritimus* and *E. primus* by having the area of the episternum posterior of the anterodorsal margin of the metepisternum smooth and glabrous (gently crenulate and setose in *E. maritimus* and *E. primus*); from males of *E. whartoni* by the umbilicate anterodorsal margin of the mesopleuron (rugulose in *E. whartoni*), and the presence of micropores on T4 –T9 (present but barely visible in *E. whartoni*).

Redescription.—**Female**. As in description of genus, with antennae of female with 12 flagellomeres; median mesoscutal impression deep, short, notch-like (Fig. 1C); mesoscutum distinctly transversely rugulose across entire surface; dorsal-anterior margin of mesopleuron umbilicate, transitioning to rugulose ventrally; mesopleural triangle setose; metapleuron evenly covered with long setae, with denser setae in ventral setal pit; metasomal T4 –T9 with distinctly visible micropores (cf. Fig. 1F), dense setal band present along posterior margin of T8; metafemora and metatibiae orange; pro-, meso- and metatarsomeres dark orange to brown.

Male. As in female but with 13 flagellomeres; flagellomere 1 as long as fourth antennal segment, laterally excavated, expanded slightly on distal end.

Material examined.—Holotype. [first label] "Idyllwild, Cal.", [second label] "1622", [third label] "Type No. 27228 U.S.N.M.", [fourth label] "*Euceroptres montanus* Weld". The type is a female in good condition, deposited in USNM. *Additional material.* Allotype. USA: *CALIFORNIA*. **Riverside Co**. Idyllwild, April [19]23 (remaining label data as in holotype labels), 1 male (USNM). Paratypes. USA: *CALIFORNIA*. **Riverside Co.** Idyllwild, April [19]23 (remaining label data as in holotype labels), 17 males, 19 females (USNM). **Trinity Co**. Big Bar, cut out Dec [19]23, code 1622, 1 female (USNM). **El Dorado Co**. Kyburz, code 1622 [no other data available], 1 female (USNM). *OREGON*. **Douglas Co**. Canyonville, June 3 [no year recorded], code 1622, Beut.[enmueller] Coll., rec'd 1935, 2 males, 4 females (USNM). **Josephine Co**. Holland, April [19]23, code 1622, 1 male (USNM). Non-types. USA: *CALIFORNIA*. **Santa Clara Co.** Los Gatos, Hopkin's number 15922[h], reared various dates between 7–21 May 1919 from *Quercus chrysolepis* Liebmann, R.D. Hartman, collector, 5 males, 4 females (USNM).

Note: Weld (1926) recorded two specimens of this species recorded from Kern Co., CA, from the 'Museum', presumably the USNM; these specimens were not located.

Distribution.—Western United States, from southern Oregon in the north to southern California in the south.

Biology.—Reared from the cynipid gall inducer *Andricus truckeenis* (Ashmead) on *Quercus chrysolepis* Liebm. in CA. This data taken from Weld (1926); no specimens were found in the USNM with associated host data.

Euceroptres primus Ashmead, 1896
Fig. 2A & 2E

Diagnosis.—Females distinguished from *E. montanus* and *E. maritimus* by possessing 11 flagellomeres (12 in *E. montanus*, 10 in *E. maritimus*) and lacking micropores on metasomal T4 through T9 (males and females). *Euceroptres whartoni* also has 13 antennal segments in the female, but *E. primus* can be separated from *E. whartoni* by the short median mesoscutal impression

(elongate,1/4–1/3 length of mesoscutum in *E. whartoni*; compare Fig. 2A with 2C) in both males and females; *E. primus* also lacks micropores on metasomal T4–T8 (faintly visible in *E. whartoni*).

Redescription.—**Female**. As in description of genus, with antennae of female with 11 flagellomeres); median mesoscutal impression deep, short, notch-like (Fig. 2A); mesoscutum distinctly transversely rugulose across entire surface; dorsal-anterior margin of mesopleuron gently rugulose, setose; mesopleural triangle setose; metapleuron evenly covered with long setae, anterior margin of episternum gently rugulose, occasionally glabrous; dense setae in ventral setal pit; metasomal T4–T9 without visible micropores (cf. Fig. 1E), dense setal band lacking along posterior margin of T-8 (cf. Fig. 1E); metafemora and metatibiae orange; pro-, meso- and metatarsomeres dark orange to brown.

Male. As in female but with 13 flagellomeres; flagellomere 1 as long as fourth antennal segment, laterally excavated, expanded slightly on distal end.

Material examined.—For the purposes of nomenclatural stability, the female specimen in the USNM, currently labeled 'type #3286' is designated as lectotype. Lectotype. [first label] "Through C.V. Riley", [second label] "2640, scrub oak, Whitfelt, Georgiana, Fla., Mar 24 –[18]82, [third label] "Type No. 3286, U.S.N.M., [fourth label] '*Euceroptres primus* Ashm.", [fifth label] Lectotype designation. The lectotype is a female in good condition, deposited in USNM. *Additional material.* Paralectotypes. USA: *FLORIDA*. **Brevard Co.** Georgiana, through C.V. Riley, 2640, scrub oak, Whitfelt, Georgiana, Fla., Mar 24 –[18]82, 1 male (USNM) [this specimen was included in Ashmead's original description]; Georgiana, through C.V. Riley, 2640, scrub oak, Whitfelt, Georgiana, Fla., Mar 7 –[18]82, 1 female (USNM). *MASSACHUSETS*. Merrimac River, "780P", through C.V. Riley, 3 July, 1883, ex *Quercus alba* L., 2 females (USNM). Non-types. USA: *VIRGINIA*. **Fairfax Co.** Falls Church, Minor's Hill, Hopkin's number 8489[b], reared 24 Jun – 11 Jul 1912, ex *Quercus alba* L. Wm. Middleton, collector, 5 males, 7 females (USNM); Falls Church, Hopkin's number 8489[c], reared 24 Jun 1912, ex *Quercus alba* L., Wm. Middleton, collector, 4 males (USNM); Falls Church, Hopkin's number 8491[a], reared 29 Jun 1912, ex galls of *Callirhytis papillatus*, Wm. Middleton, collector, 4 males, 4 females (USNM); Falls Church, Hopkin's number 12059, reared 25 Jun 1914, ex *Quercus alba* L., Wm. Middleton, collector, 1 male (USNM); Falls Church, Kearney, Hopkin's number 12069[a], reared 27 Jul 1914, ex *Quercus minor* (Marshall) Sarg., Wm. Middleton, collector, 1 male (USNM); Falls Church, Hopkin's number 13600, reared 26 Apr 1915, ex galls of *Andricus flocci*, Wm. Middleton, collector, 4 males (USNM); Falls Church, Kearney, Hopkin's number 12069[a], reared 27 Jul 1914, ex *Quercus minor* (Marshall) Sarg., Wm. Middleton, collector, 1 male (USNM).

Distribution.—Eastern United States, from Maryland in the north to Florida in the south.

Biology.—Reared from *Andricus quercus-futilis* (Osten-Sacken) and *Andricus quercus-flocci* (Walsh) on *Quercus alba* L.; also reared from an unknown cynipid host on *Quercus stellata* Wangenheim. Weld (1926) also records this species from petiole galls on *Quercus stellata* from Rosslyn, VA but these specimens could not be located in the USNM.

Euceroptres whartoni Buffington & Liljeblad, new species

Figs 1E & 2C–D

Diagnosis.—Females can be distinguished from *E. montanus* and *E. maritimus* by the possession of 11 flagellomeres (12 in *E. montanus*, 10 in *E. maritimus*) and the lack of distinct micropores on metasomal T4 through T9 (Fig. 1E) (males and females); distinguished from *E. primus* by the presence of an elongate median mesoscutal impression (short and notch-like in *E. primus*; *viz.* Fig. 2A & 2C).

Description.—**Female**. As in description of genus, with antennae of female with 11 flagellomeres; median mesoscutal impression deep, elongate, reaching 1/4 to 1/3 length of mesoscutum (Fig. 2C); mesoscu-

tum distinctly transversely rugulose anteriorly, less striate posteriorly; dorsal-anterior margin of mesopleuron shagreen to gently rugulose, setose; mesopleural triangle setose; metapleuron evenly covered with long setae, anterior margin of episternum gently rugulose, frequently glabrous; dense setae in ventral setal pit; metasomal T4 –T9 without visible micropores (Fig. 1E), dense setal band lacking along posterior margin of T8 (cf. Fig. 1E); metafemora and metatibiae orange; pro-, meso- and metatarsomeres dark orange to brown.

Male. As in female but with 13 flagellomeres; flagellomere 1 as long as fourth antennal segment, laterally excavated, expanded slightly on distal end.

Etymology.—Named in honor of our mentor and friend, Robert Wharton.

Material examined.—Holotype. [first label] Hopk. U.S. 10767ς, [second label] reared Mar. 26.21 [26 Mar 1921], *Quercus minor*, [fourth label] Denton, TX, [fifth label] Marquis, R.L., coll., [sixth label] holotype, *Euceroptres whartoni* Buffington & Liljeblad. The holotype is a male in good condition, deposited in the USNM. *Additional material*. Paratypes. Same data as holotype: USA: *TEXAS*. **Denton Co**. Denton, ex triangular galls on *Quercus minor*, collected 26 Jan 1920 [emergence date not recorded], R.L. Marquis, collector, Hopkin's number 10767ς (2 males and 4 females, NHMN). Non-types. USA. *FLORIDA*. **Volusia Co**. Hopkin's number 15634g, reared 15 Oct 1922 from woolly midrib cluster galls collected 8 Dec 1919 from *Quercus laurifolia* Michx. (1 female, NMHH). *MARYLAND*. **Montgomery Co**. Plummers Island, 12 Apr 1914, W.L. McAtee, coll. (1 male, USNM). *MISSOURI*. **Stoddard Co**. 30 Mar 1938, T-10242, on peach (1 female, USNM). *VIRGINIA*. **Fairfax Co**. East Falls Church, Hopkin's number 13651i, 23 Apr 1917, reared from *Callirhytis operator* sexual generation [in Weld's hand] collected from *Quercus marylandica* Du Roi, Wm. Middleton, coll., 1 Jun 1916 (2 females, USNM). [collection data unknown] No. 2640, Apr 19.82 [(19 Apr 1882(?)], (1 male USNM); No. 2640, Apr 21.82 [(21 Apr 1882(?)], (1 male USNM); [collection data unknown] "with *A. cicatricula* Bass." [this specimen corresponds to a specimen mentioned in Weld (1926), originally determined as *E. primus*, that was originally found among the cotype material of *Cynips cicatricula* Bassett, collected from *Quercus alba* in Waterbury, CT.] (1 male, USNM).

Distribution.—Eastern and Southeastern United States, from Texas in the West to Connecticut and Maryland in the East.

Biology.—Reared from *Andricus quercus-operator* (Osten-Sacken) galls on *Quercus nigra* L. in Virginia. A second rearing record is circumstantial at best: specimens mentioned above that were associated with *Cynips cicatricula* Bassett (=*Andricus quercuspetiolicola* (Bassett)) were bred from *Quercus alba* L. *Quercus nigra* and *Q. alba* belong to different sections of *Quercus* subg. *Quercus*; the former is a red oak wheras the latter is a white oak. Not much is known about the host-specificity of *Euceroptres*. If they are anything like the cynipid inquilines or even true parasitoids, these host records could very well be correct. On the other hand, no Nearctic species of oak gall wasps is known to attack hosts from more than one oak section (Stone et al. 2002).

DISCUSSION

Two distinct lineages of *Euceroptres* emerged from this study. One, composed of *E. maritimus* and *E. montanus*, appears to be restricted to the western Nearctic Region, chiefly collected in CA and OR. The second lineage comprises *E. primus* and *E. whartoni* and occurs in the eastern and southeastern Nearctic Region. In fact, this latter lineage may be rather widespread throughout the southeast. Within *Euceroptres*, based on characters described herein, the following set of relationships is proposed: ((*E. montanus* + *E. maritimus*)(*E. primus* + *E. whartoni*)). The first clade (*E. montanus* + *E. maritimus*) is united by the shared presence of micropores on the metasoma (Fig. 1F) and a distribution restricted to the western Nearctic. The second clade, composed of (*E. primus* + *E. whartoni*) are united by the shared presence of 13 antennal segments in the female, the overall reduction in micro-

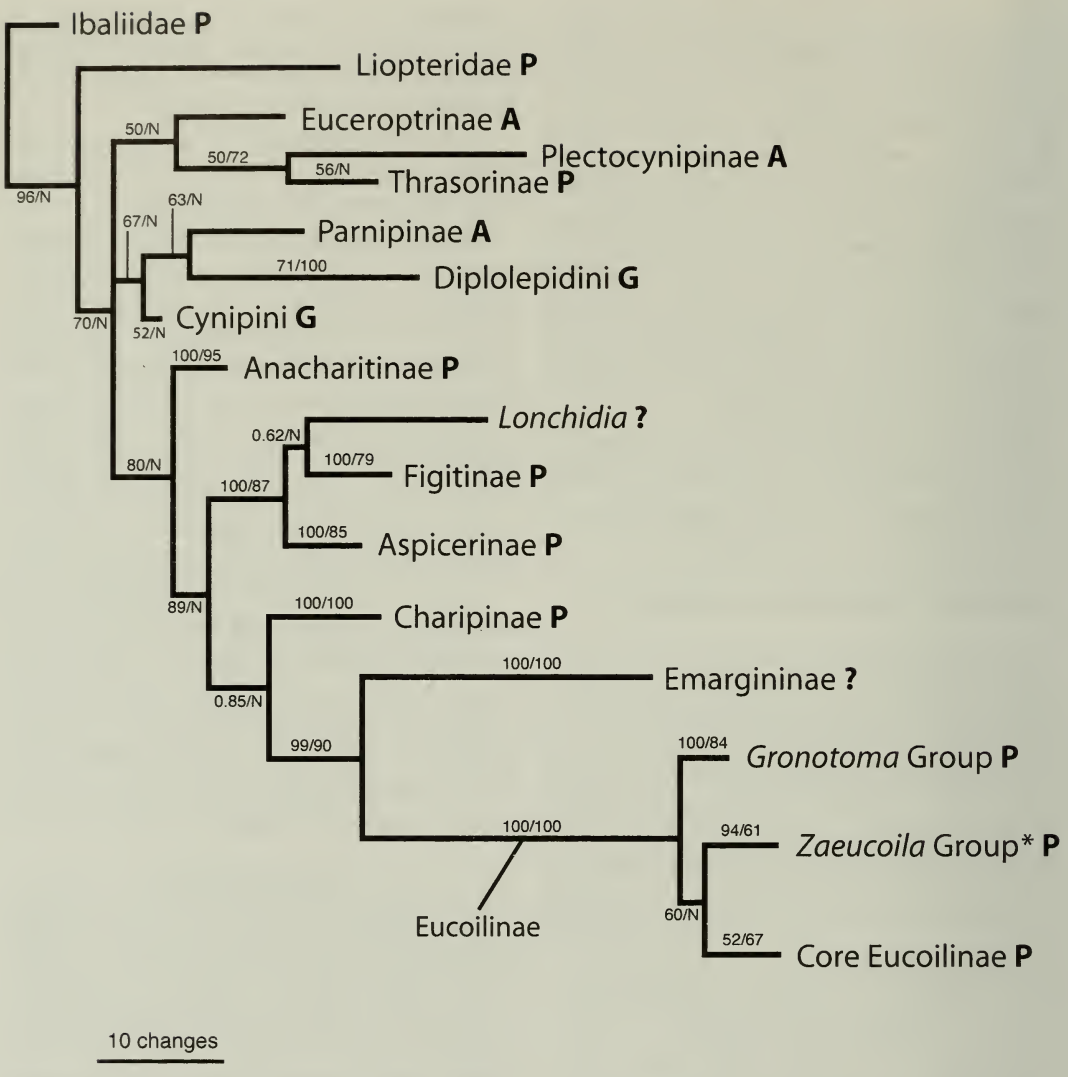

Fig. 3. Phylogram of Figitidae resulting from Bayesian analysis of 28S D2&D3 and 18S rRNA, COI and morphology (see *Materials and Methods*). Analyses of the same data using parsimony result in nearly the same tree (see below); '*' at the *Zaeucoila* Group indicates this clade is sister-group to the *Gronotoma* group in the parsimony analysis. Letters after terminal names refer to: A, agastoparasite; G, gall inducer; P, non-agastoparasite. Numbers on branches indicate branch support in the form of Bayes posterior probability/parsimony bootstrap support; 'N' indicates less than 50% support was recovered for that node; Bayesian posteriors calculated using 50% majority rules consensus. Parsimony analysis resulted in 375 trees distributed across 46 islands; CI=.18, RI=.62.

pores on the metasoma, and a distribution encompassing the eastern/southeastern Nearctic Region.

A striking symplesiomorphy of *Euceroptres* is the presence of a very well developed lateral pronotal carina (Fig. 1A). As stated earlier, this character is shared with Liopteridae (Ronquist 1995b) and Stolamissidae (Liu et al. 2007), the figitids Aspicerinae, Parnipinae, the *Gronotoma* group of Eucoilinae (Buffington et al. 2007) and a few Cynipidae (Ronquist 1995b).

Conclusive evidence for the exclusion of *Euceroptres* from Thrasorinae was provided in two independent studies (Ros-Farre and Pujade-Villar 2007, Buffington et al. 2007)

as well as this study (Fig. 3). With the erection of Euceroptrinae, a system of small subfamilies, sister to the remaining higher taxa within Figitidae, reflects a rather complicated evolutionary history (Fig. 3). It should be noted, however, that the branch support for (Euceroptrinae (Plectocynipinae+Thrasorinae)) is weak in both parsimony and Bayesian analyses (Fig. 3). As stated by Buffington et al. (2007), additional data are required to definitively resolve these relationships; data collection for additional species of Plectocynipinae and Thrasorinae is currently underway (Buffington and Scheffer unpublished).

The association of these lineages with gall-inhabiting hymenopterous hosts begs the intriguing possibility that phytophagous cynipids arose from a rather diverse range of proto-figitids attacking various gall-inducing hosts (Ronquist and Nieves-Aldrey 2001). These lineages also may represent the origins of agastoparasitism within Cynipoidea, though Nylander (2004) and Melika (2006) suggest inquilinism arose independently in Cynipidae numerous times. Certainly within Figitidae, agastoparasitism is the plesiomorphic life-history strategy (Fig. 3, terminals lettered 'A', agastoparasites; 'G', gallers; 'P', non-agastoparasites), with the more derived Thrasorinae shifting to chalcidoid hosts (Ros-Farré and Pujade-Villar 2007, Buffington et al. 2007, Buffington submitted).

Although the cynipid hosts of *Euceroptres* gall only 5 or 6 species of *Quercus*, their oak hosts could hardly be a more diverse sample coming from the Nearctic (Table 1). All three sections of *Quercus* subgenus *Quercus* are represented, the missing fourth being the exclusively Palearctic section *Cerris* (Manos et al. 1999). This could be just a random sample from a few species attacking a number of *Andricus* gall wasps. If, however, species of *Euceroptres* are more host-specific, it lends further support to the idea that this genus was once a more species rich group of which only a few scattered lineages have survived to date. Liu et al. (2007) date the split of cynipids and figitids to at least the early Cretaceous, providing evidence that even 'neo-eucoilines' ('core' Eucoilinae of Fontal-Cazalla et al. 2002; *Zamischus* group of Buffington et al. 2007) were present in the mid-Cretaceous. These data suggest the Figitidae are indeed an old lineage, and members of these depauperate ancestral lineages may represent so-called 'living fossil' taxa, giving us a tantalizing opportunity to look into the evolutionary history of this diverse group of parasitoid Hymenoptera.

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